

ATTRACTION OF INSECTS TO
ODORANT SOURCES IN A WAREHOUSE

By

RICHARD WENDELL MANKIN

A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL
OF THE UNIVERSITY OF FLORIDA IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1979

ACKNOWLEDGEMENTS

During this study I was employed by the U.S. Department of Agriculture, Insect Attractants, Behavior, and Basic Biology Laboratory in Gainesville, Fla. I thank the director, Dr. Darrell Chambers and my supervisors, Dr. P. S. Callahan and Dr. J. C. Webb for their cooperation and support services.

I also thank Drs. K. W. Vick, J. C. Coffelt, R. Pepinski, and A. Nevis for their advice and encouragement, and Drs. M. S. Mayer, J. L. Nation, J. Anderson, and R. Cohen for serving on my committee. Cheryl Steward and Maribeth Michaud provided assistance with the bioassays.

Special thanks go to Dr. P. S. Callahan, Committee Chairman and Dr. M. S. Mayer for their technical, editorial, and advocacy efforts.

Lastly, I salute the insects who bravely but unknowingly donated their lives for the sake of the project.

TABLE OF CONTENTS

	PAGE
ACKNOWLEDGEMENTS.....	ii
ABSTRACT.....	iv
INTRODUCTION.....	1
CHAPTER	
ONE ANEMOTACTIC RESPONSE THRESHOLD OF THE INDIAN MEAL MOTH, <i>Plodia interpunctella</i> (HUBNER) (LEPIDOPTERA:PYRALIDAE), TO ITS SEX PHEROMONE.....	3
Methods and Materials.....	4
Results.....	12
Discussion.....	18
TWO AN INSECT ATTRACTANCE MODEL.....	22
Case I: Molecular Diffusion.....	23
Case II: Dispersal in Airflow of Zero Average Velocity.....	35
Case III: Dispersal in Airflow of Constant Average Velocity.....	36
Results.....	40
Discussion.....	53
CONCLUSIONS.....	58
APPENDIX.....	60
REFERENCES.....	63
BIOGRAPHICAL SKETCH.....	71

Abstract of Dissertation Presented to the Graduate
Council of the University of Florida in Partial
Fulfillment of the Requirements for the
Degree of Doctor of Philosophy

ATTRACTION OF INSECTS TO
ODORANT SOURCES IN A WAREHOUSE

By

Richard Wendell Mankin

August 1979

Chairman: P. S. Callahan

Major Department: Entomology and Nematology

Methods are presented for determining the behavior of an insect stimulated by an attractant source in still air, turbulent air of zero average velocity, and turbulent or laminar air currents of constant, nonzero average velocity.

Plodia interpunctella (Hubner) (IMM) is the chief test insect for application of the methods. To use the IMM, it was first necessary to measure the effect of different concentrations of the sex pheromone (Z,E)-9,12-tetradecadien-1-ol acetate on the upwind anemotactic behavior of the male. A bioassay was performed to obtain stimulus-response regression lines at 23°C and 34°C. The regression lines were analyzed by a new procedure that accounts for control responses in the absence of pheromone and also peak responses well below 100% at pheromone concentrations considerably above the lowest detectable levels. On the basis of this analysis,

the upwind anemotactic threshold is 1.34×10^6 molecules/cm³ at 23°C and 1.65×10^4 molecules/cm³ at 34°C. Departures from the 2 lines occurred at the highest pheromone concentrations tested, near 10^8 molecules/cm³. This suggests that the upwind anemotactic behavior changes qualitatively above an altered-behavior threshold about 2 orders of magnitude above the upwind anemotactic threshold. The decreased response at 23°C compared to 34°C suggests that flight in response to pheromonal stimulation is inhibited at cool temperatures.

Calculations of the above methods using the IMM thresholds and similar thresholds of other insects indicate the following: (1) In a warehouse a searching insect is likely to be attracted to a calling insect if it comes within an attraction space, a sphere surrounding the calling insect, ranging from 0.4 to 2.4 m in radius. (2) The attraction spaces of typical sex pheromone traps, emitting pheromone at rates greater than 0.01 ng/sec, extend beyond the boundaries of a 10 x 10 x 10-m warehouse. (3) The searching behavior of an attracted insect is likely to be altered from an extensive to an intensive pattern if it comes within a calling insect's altered-behavior space, a sphere 6-60 cm in radius. (4) The altered-behavior space of a trap emitting 0.76 ng/sec extends beyond the boundaries of a 10 x 10 x 10-m warehouse. (5) Pheromone does not fall unless it is emitted along with a large amount of a high-vapor pressure solvent. The calculations are used in support of the following:

(1) The effect of an adsorptive surface on the odorant concentration after an extended period of emission is negligible except at positions near the surface. (2) Traps with odorant sources of small dimensions have greater trapping efficiency than otherwise identical traps with sources of large dimensions. (3) The function of the altered-behavior threshold may be to increase the probability of a stimulated insect finding a calling insect. Additional applications and hypotheses are also presented for conditions outside a warehouse.

INTRODUCTION

The probability of an insect finding an attractant source is determined by the pattern and intensity of its searching behavior, which are strongly affected by the attractant concentration and the dynamics of the airflow (Roelofs, 1975; Shorey and McKelvey, 1977). Several different mathematical expressions of these relationships have been presented in insect attractance models by Wright (1958), Bossert and Wilson (1963), Bossert (1968), Hartstack et al. (1976), Hirooka and Suwanai (1976), Aylor (1976), Aylor et al. (1976), Nakamura (1976), Nakamura and Kawasaki (1977), and Roelofs (1978). None of these models considers jointly 3 problems frequently encountered in a warehouse environment: deposition of attractant onto exposed surfaces, restricted dispersal of attractant near obstructions, and the complicated rapidly changing pattern of the airflow. The need for methods to treat such problems is demonstrated by the growing number of sex pheromone trapping experiments involving postharvest pests (Sower et al., 1975; Barak and Burkholder, 1976; Read and Haines, 1976; Von Reichmuth et al., 1976, 1978; Shapas, 1977; and Vick et al., 1979).

Although the model derived below is applied primarily to attraction in a warehouse, it also applies to field and

forest environments, incorporating many elements of previous models. Like the Bossert and Wilson (1963) model it can be used to calculate an odorant source's attraction space, a zone where the average odorant concentration is above a perceptual or behavioral threshold, under either still air or steady airflow conditions. Like the Aylor (1976) model it treats the effects of turbulence in detail. Like the Roelofs (1978) model it includes the effects of an altered-behavior threshold, occurring about 3 orders of magnitude above the perceptual threshold. Moreover, it considers adsorption processes, boundary positions, gravitation, and the instantaneous structure of the odorant plume.

The model is tested using the Indian meal moth (IMM), Plodia interpunctella (Hubner) (Lepidoptera:Pyralidae). A bioassay to determine parameters included in the model is presented in Chapter I. The model is derived and applied to several problems in Chapter II.

CHAPTER ONE
ANEMOTACTIC RESPONSE THRESHOLD OF THE INDIAN MEAL MOTH,
Plodia interpunctella (HUBNER) (LEPIDOPTERA:
PYRALIDAE), TO ITS SEX PHEROMONE

An insect's threshold of response to sex pheromone is an important parameter of many uses in olfactory physiology (Kaissling, 1971) and applied entomology (see Chapter II). The IMM is a widespread postharvest pest whose pheromonal physiology has been studied extensively, but whose behavioral response to pheromone has not been quantified in exact units. IMM populations have been monitored using sex pheromone traps (Vick et al., 1979); thus, there is some practical interest in the incorporation of an exactly quantified response threshold for IMM into a trapping model. Of all the measurable thresholds, the one most appropriate for use in a trapping model is the threshold for upwind anemotaxis, because an insect stimulated to fly has a greater likelihood of being captured by a trap than an insect stimulated merely to respond orthokinetically (by antennal vibration or wing flutter). To compare the pheromonal response of the IMM with that of other insects and to determine a representative threshold for use in postharvest pest trapping models, the upwind anemotactic response of the male IMM was measured at 23°C and 34°C.

Methods and Materials

Insects

Male pupae were transferred at 3-day intervals from a laboratory colony (Silhacek and Miller, 1972) to an environmental chamber at 27°C and 60% RH on a 16:8 L:D cycle (20-W GE #F201-T2-CW light source in photophase, <0.05 lux in scotophase). During the photophase, groups of 50-75 newly-emerged adults were placed into plastic boxes (20 x 10 x 10 cm) with screen lids, where they remained without food or water until testing began 3-5 days later.

Pheromone

The IMM pheromone, (Z,E)-9,12-tetradecadien-1-ol acetate (ZETA), purchased from Storey Chemical Co., Willoughby, OH, was purified twice before use by elution with benzene through a column of 25% AgNO₃ on silicic acid. Gas and thin layer chromatographic analyses indicated that the purified ZETA was at least 99% pure. Between tests the ZETA was stored at -25°C.

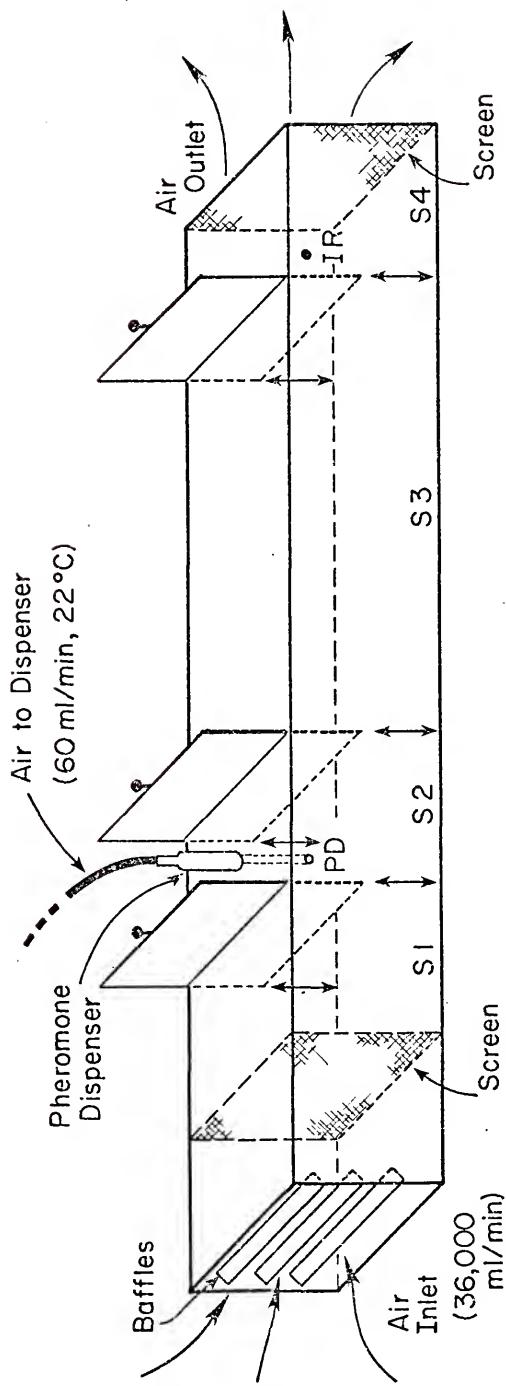
The ZETA was dispensed from a glass tube made by reducing the unground ends of a 14 cm long by 2 cm ID assembly of 24/40 ground-glass joints to 0.5 cm ID (Mayer, 1973). About 5 min before a test the inside of the assembly was coated evenly with a 0.5 ml aliquot of ZETA in diethyl ether. The levels of ZETA in the dispenser ranged from 0 (control) to 10⁵ ng. After the ether evaporated, the assembled tube was stoppered until the test began.

Olfactometers

The bicassay was done in 3 ($0.3 \times 0.3 \times 3.5$ m) olfactometer tunnels described previously by Mayer (1973). Each tunnel had 4 closable sections designated S1-S4 in upwind to downwind order in Fig. 1. S1, S2, and S4 were 56 cm long, and S3 was 140 cm long. The outlet of a pheromone dispenser was placed near the center of S2 at point PD. Moths were released near the center of S4 at point IR, 3 m downwind from PD. The tunnels were supplied with filtered air (55-60% RH, 3.6×10^4 cm³/sec flow rate, 35-50 cm/sec velocity) in one of 2 temperature ranges: 22-24 or 33-35°C. Light was provided by 8, rheostat-dimmed, 60 W tungsten bulbs placed separately inside diffuser boxes spaced uniformly around the perimeter of the room at the ceiling. The average light intensity inside the tunnels was monitored at 1 lux = 1.5 mw/m².

The airflow pattern in the tunnels was depicted by smoke plumes. The plumes were produced by either passing humidified air through a dispenser tube at PD containing a cotton swab soaked in a 1:1 mixture of TiCl₄ in CCl₄, or by substituting a smoke generator (TEM Eng., Ltd., Crawley, England) for the tube. Both methods generated plumes that quickly dispersed into less and less distinct filaments. Within 2 m downwind from PD, there was no more than a 4:1 variation in the observed smoke density across the tunnel's cross-section. Because pheromone molecules disperse at

Figure 1. Diagram of olfactometer used in bioassay: PD is the pheromone dispensing point, IR is the insect release point, and S1-S4 are closable sections.



OLFACTO METER

least as fast as smoke particles (Miller and Roelofs, 1978), these observations indicate that the average pheromone concentration at IR is reasonably approximated by the ratio of the dispenser's emission rate to the tunnel's airflow.

Bioassay Procedure

After preliminary experimentation the following procedure was standardized: (1) During the first 2-5 h of the scotophase, 40-50 male IMM were loaded into a screen cage (17.5 x 20.3 x 25.4 cm) and placed at point IR in a tunnel. (2) A period of 0.5-3 h ensued to allow acclimation. (3) A dosed, stoppered dispenser tube was placed at PD. The stoppers were removed and filtered air (22°C , 60 ml/min) was passed through the tube. (4) Within 10 sec the holding cage was opened allowing the IMM freedom to move within the tunnel. After an additional 60 sec the sections were closed and the number of IMM in each section was counted. The upwind anemotactic response was estimated by the fractional response, Fr, the number in S2 and S3 divided by the total number in S1-S4. (5) The dispenser tubes and the holding cages were washed and baked for 12 h at 200°C after each use, and the tunnels were cleaned with ethanol twice a week to minimize the possibility of pheromonal contamination.

The bioassay had an incomplete block design. A treatment was one of 20 combinations of 2 temperatures (23° , 34° C) and 10 tube doses (blank control, 0.3, 1, 10, 10^2 , 10^3 , 3×10^3 , 10^4 , 3×10^4 , and 10^5 ng). Tests were also done

at 17° C using 10^4 ng doses, but were discontinued because of the negligible response. A block was a set of 6 treatments tested on a given day at a given temperature. One of the 6 was always a blank, placed randomly within the block. At least 3 other treatments were randomized within the remainder of the block to eliminate day-to-day variation in the IMM response from comparison of the treatments.

Response Analysis

The standard procedure for calculating a behavioral threshold is to adjust the fractional response for the control (Abbot, 1925) and then to analyze the regression of the probit adjusted response on dose (Finney, 1971). However, the stringency of the upwind anemotactic response criterion kept the maximal response in this bioassay well below 100%, contrary to the normal distribution of response frequency assumed in probit analysis. If the response frequency were normally distributed there would be a concentration above which the response would approach 100%, just as there would be a concentration below which the response would approach 0%. The standard Abbot's correction accounts only for deviations from the normal distribution at the 0% limit. By contrast, the following 3-step procedure accounts for deviations at both the 0% and the 100% limits, and is more generally applicable to quantal bioassays.

First, the response was transformed to probit coordinates using the normalizing equation (Box et al., 1978):

$$Nr = \text{Prob} \left(\frac{100(Fr-Frc)}{Frm-Frc} \right) \quad (I.1)$$

Where: Nr is the normalized response, in units of probits;
 Fr is the uncorrected fractional response;
 Frc is the average fractional response in the control;
 Frm is the maximum average fractional response at the given temperature;
 Prob is the integral operator (Finney, 1971).

In the usual Abbot's correction, $Frm = 1$. Next, the normalized responses from Eq.I.1 were fitted by the standard probit analysis to the equation:

$$Nr = I + S \text{ Log } (DD) \quad (I.2)$$

Where: I is the temperature-dependent intercept, in units of probits;
 S is the temperature-dependent slope, probits μg^{-1} ;
 DD is the dispenser dose, μg .

Finally the Nr-DD regression line, Eq. I.2, was converted to Abbot's-corrected coordinates using the inverse transformation:

$$Pr = \left(\frac{Fr_m - Fr_c}{1 - Fr_c} \right) Probit^{-1} (Nr) \quad (I.3)$$

Where: Pr is the Abbot's corrected % response (Abbot, 1925);
 $Probit^{-1}$ is the inverse probit operator.

To convert behavioral thresholds measured in units of μg dose to thresholds in the more practical units of molecules/cm³, the relationship between a dispenser tube's dose and the concentration in the tunnel must be quantified. This relationship was determined by a calibration of the tube's emission rate.

Calibration of Dispenser

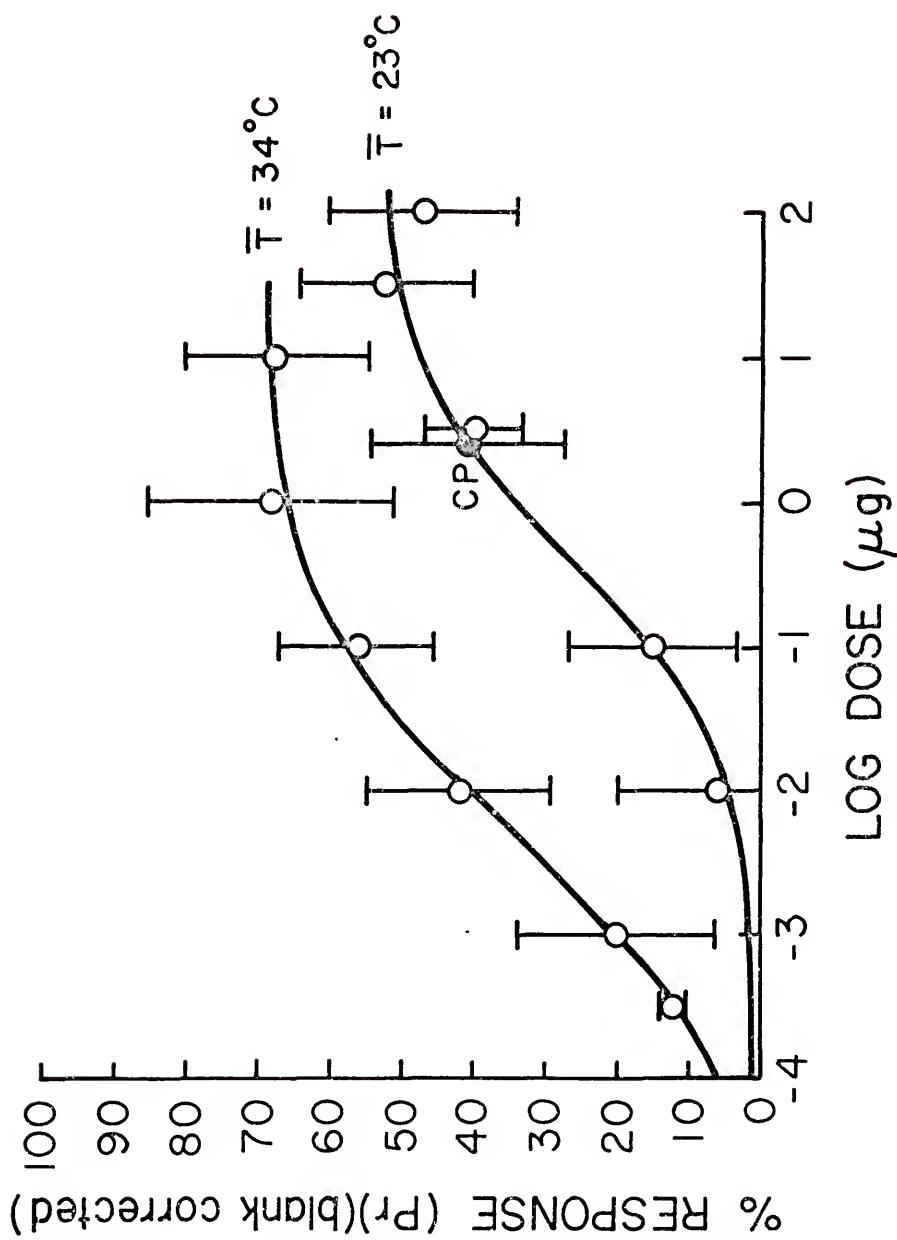
At room temperature pheromone volatizes from a dispenser tube at a rate proportional to the initial dose and inversely proportional to the duration of emission. To investigate this relationship, emissions from dispenser tubes loaded with the pheromone (Z)-7-dodecen-1-ol acetate (Z7AC) were collected in 1 mm ID x 30 cm long glass, or 1 mm ID x 70 cm long, stainless steel capillaries using a thermal gradient GLC capillary collector (Brownlee and Silverstein, 1968), and quantified by standard gas chromatographic procedures. The results indicated that over doses of 1-175 μg

and emission durations of 15-180 sec, the emission rate was a constant proportion of dose, independent of time (Mayer and Mankin, in preparation). The constant of proportionality between the dose and the output of ZETA, Ke, was measured by a separate calibration bioassay at 23°C, similar to that described 2 sections previously, except for step 3 which was changed to: (3') a polyethylene cap emitting ZETA at a rate of 0.13 ± 0.07 SE ng/sec, as measured by the method of Vick et al. (1978), was suspended at PD. The tube dose evoking the same average blank-corrected response as the cap was divided into the measured emission rate of the cap to estimate Ke.

Results

The fraction of tested IMM attracted to a dispenser was sigmoidally proportional to the logarithm of the dose, as shown in Fig. 2, and uniformly higher at 34°C than at 24°C. Each data point in Fig. 2 represents the mean of 8-10 treatment replications, with the vertical line indicating the 95% confidence interval. The slope and intercept parameters of each regression line are listed in Table 1. Both the slopes and the intercepts of the 2 lines are statistically different ($t = 4.9$ p < 0.01, and $t = 57.3$ p < 0.001, respectively). The good fit of the regression lines to the data, indicated by the low χ^2 values (p > 0.5 at 23°C and p > 0.75 at 34°C), supports the use of the modified probit analysis for interpreting pheromonal stimulus-response relationships.

Figure 2. Abbot's corrected IMM attraction response to ZETA, Pr', at different dispenser doses and different temperatures. The regression lines are derived from Eq. I.3 in the text. Point CP is the response obtained using the calibrated cap emitting 0.13 ng/sec. Each data point represents the mean of 8-10 treatment replications, with the vertical line indicating the 95% confidence interval.



The pheromone concentration in an olfactometer at the point of insect release, IR, was calculated by assuming that the dispenser output disperses uniformly in the $3.6 \times 10^4 \text{ cm}^3/\text{sec}$ airflow (Methods: Olfactometer section). The dispenser output is the product of the dispenser dose, DD, and the constant of proportionality between dose and output, Ke, which can be estimated using point CP in Fig. 1, the intersection of the 23°C dose response regression line with the mean Abbot's corrected % response for 8 cap dispenser test replications. The Ke is the ratio of the cap's emission rate to the tube dose at CP: $0.13 \text{ ng sec}^{-1}/2500 \text{ ng} = 5.2 \times 10^{-5} \text{ sec}^{-1}$. Thus, the concentration at IR is

$$\begin{aligned} C &= 5.2 \times 10^{-5} \text{ sec}^{-1} / 3.6 \times 10^4 \text{ cm}^3 \text{ sec}^{-1} \text{ DD} \\ &= 1.44 \times 10^{-9} \text{ cm}^{-3} \text{ DD} \end{aligned} \quad (\text{I.4})$$

The threshold of upwind anemotaxis for a male IMM was calculated using Table 1 and Eq. I.4. Following the standard procedure of probit analysis, the threshold was defined as the concentration at which the normalized fraction of response was 0.5 (5 in probit units). Using the 2 values of DD for $\text{Nr} = 5$ in Eq. I.4 gives thresholds of 1.34×10^6 and $1.65 \times 10^4 \text{ molecules cm}^{-3}$ (2.12×10^{-15} and 2.74×10^{-17} molar) at 23°C and 34°C , respectively, which are compared with other reported thresholds in Table 2.

Table 1. Analysis of the dose-response regression lines in Fig. 1. Symbols I, S, Nr, and DD are defined in Eqs. I.1-2.

Parameter	Temperature (°C)	
	23	34
I (probits)	5.38	6.81
I Standard error	0.115	0.070
S (probits/ μ g)	0.405	0.341
S Standard error	0.048	0.030
DD for Nr = 5 (μ g)	3.88	0.0048
Upper limit DD (95%)	13.5	0.0079
Lower limit DD (95%)	0.054	0.0028
Degrees of freedom	3	4
χ^2	1.66 P>0.5	1.77 P>0.75

Table 2. Pheromonal behavioral thresholds of some insects.
 Other thresholds are reported in Kaissling (1971).
 The behavioral response criterion was upwind
 anemotaxis for the IMM and orthokinesis for the
 other insects.

Insect:	Pheromone	Threshold concentration (10^{-3} mol) $\frac{3}{cm}$	References
<u>Bombyx mori:</u>			
17°C	(E,Z)-10,12-hexadecadien-1-ol	20	Kaissling &
21°C		10	Priesner 1970
<u>Trichoplusia ni:</u>			
24°C	Z7AC	8	Sower et al. 1971
<u>Plodia interpunctella:</u>			
34°C	ZETA	16.5	
23°C	ZETA	1340	Chapter I
<u>Trogoderma glabrum:</u>			
27°C	(-)-14-methyl-(Z)-8-hexadecenal	2300	Shapas 1977
<u>Lymantria dispar:</u>			
25°C	(Z)-7,8-epoxy-2-methyl octadecane	115	Aylor et al. 1976

Discussion

The results of the bioassay demonstrated that the upwind anemotaxis threshold of the male IMM for its sex pheromone is similar to the thresholds of other insects for their respective sex pheromones. Inspection of Table 2 reveals that the IMM 34°C upwind anemotactic threshold is similar to the Bombyx mori (Linnaeus) and Trichoplusia ni (Hubner) orthokinetic thresholds, while the 23°C threshold is closer to the Trogoderma glabrum (Herbst) and Lymantria dispar (F.) orthokinetic thresholds. By contrast, human olfactory thresholds generally range from 10^8 to 10^{11} molecules/cm³, while the theoretical limit of olfactory perception is about 200 molecules/cm³ (Kaissling, 1971). Because the lowest thresholds in Table 2 approach this limit, it can be assumed that these behavioral thresholds approximate the corresponding perceptual thresholds. In addition, all of the reported sex pheromone behavioral thresholds are within 4 orders of magnitude of this lower limit. Thus, if a trapping model is applied to any insect whose threshold for attraction to sex pheromone is unknown, the threshold can be estimated to lie in the range of 10^3 to 10^6 molecules/cm³.

Dose Dependence of the Attraction Response

In most respects, the attraction responses in Fig. 2 follow the standard sigmoidal relationship obtained with many other insects (Schneider et al., 1967; Kaissling and Priesner, 1970; Sower et al., 1971; Mayer, 1973; Shapas, 1977).

In particular, the change from 0 to 100% normalized response occurs within about 4 concentration decades. However, departures from the sigmoidal relationship appear to occur at the highest tested doses. At 34°C the response to 10 µg is lower than the response to 1 µg, and at 23° the response to 100 µg is lower than the response to 30 µg. Neither of these decreases are statistically significant, but they are systematic. In addition, similar decreases in response with increasing dose have been reported in olfactometer studies of other insects (Mayer, 1973; Fuyama, 1976; Hawkins, 1978), and decreases in trap catch with increasing dose have been reported in field trapping studies (Wolf et al., 1967; Shorey et al., 1967; Gaston et al., 1971; Vick et al., 1979). This suggests that the observed decreases are not statistical irregularities.

One hypothesis for the response decrement is that the pheromone could be contaminated with a slight amount of the homolog (Z,Z)-9,12-tetradecadien-1-ol acetate, which is known to act as an inhibitor of attraction behavior (Vick and Sower, 1973). Such contamination is unlikely, however, because the purified pheromone was found to be at least 99% pure by gas and thin layer chromatography. More likely, the observed decrease is the effect of an altered-behavior threshold (Roelofs, 1978). The relationship between the upwind anemotactic threshold and the concentration at which the response begins to depart from the sigmoid supports this

hypothesis. According to Roelofs (1978), the altered-behavior threshold of an insect is typically about 3 orders of magnitude above the orthokinetic threshold, which is somewhat lower than the upwind anemotactic threshold. The observed departure occurs near 10^{-5} ng/cm³, 2-3 orders of magnitude above the upwind anemotactic threshold as predicted.

Temperature Dependence of the Attraction Response

The effect of temperature on the IMM upwind anemotactic behavioral threshold is similar to that reported previously for the orthokinetic threshold of B. mori (see Table 2). The B. mori threshold shifted 0.13 log units/°C while the IMM threshold shifted 0.19 log units/°C. A related effect on the percentage mating of T. ni was reported by Shorey (1966). The most likely hypothesis for the observed increase in threshold with decreasing temperature is that the lower temperatures tend to inhibit flight in response to pheromone. Indeed, in several preliminary assays done at 17°C the IMM exhibited no response to 10 µg doses that were highly stimulatory at 23°C. This effect may be related to low temperature effects on flying activity reported in a variety of other insects (Taylor, 1963; Bursell, 1964; Sanders et al., 1978; and references therein).

The findings regarding temperature effects suggest that sex pheromone traps may capture more IMM at warm temperatures than cool temperatures. Similar effects of temperature on the pheromone trapping of other insects have

been reported by Showers et al. (1974), Marks (1977), and Coster et al. (1978). The effects of temperature on trapping are more complicated than the effects on attraction behavior, however, because the temperature also affects the rate of pheromonal emission from the trap and temperature stratification can affect the pheromonal dispersal pattern (see Chapter II). In addition, the temperature variation may have a greater influence on the behavior of some insects than the average temperature (Showers et al., 1974).

In summary, the upwind anemotactic threshold of the male IMM to its sex pheromone is similar to the sex pheromone thresholds reported for other insects. The threshold depends on temperature, mostly because the upwind anemotactic response to pheromone is inhibited at low temperatures. About 2 orders of magnitude above the behavioral threshold there may be an altered-behavior threshold that causes a modification of the attraction response.

CHAPTER TWO
AN INSECT ATTRACTANCE MODEL

The derivation of the model proceeds in stages of increasing complexity. First, the general problem of attraction to an odorant source is simplified and expressed mathematically in terms of quantifiable parameters. Then the scope and complexity of the problem are increased by examining the qualitative effects of several unquantified factors. Considerable simplification of the attraction problem is achieved by adopting the following assumptions: (1) An attractant chemical has a threshold concentration below which its probability of stimulating an insect is nil. (2) An attractant has a corresponding altered-behavior threshold concentration above which the probability of the insect finding a distant source decreases. (3) The attraction and altered-behavior thresholds depend upon the insect's species and age, the temperature, and the chemical nature of the attractant, all of which are fixed in a given application of the model. (4) The emission rate of the attractant source is constant. None of these assumptions are strictly valid under the usual modeling applications in which insect age, ambient temperature, and source emission rate vary, but they are nevertheless useful heuristically.

Because attraction and altered-behavior thresholds can be measured by bioassay, the simplified problem obtained using assumptions 1-4 is essentially solved once the attractant distribution is determined. But even this is a formidable task. The plume emitted from an attractant source disperses in a complicated pattern that depends on the characteristics of the airflow (Skelland, 1974). Three different cases will be considered in the derivation: dispersal in still air by molecular diffusion, dispersal in turbulent air currents of zero average speed and direction, and dispersal in turbulent or laminar air currents of constant average speed and direction.

Case I: Molecular Diffusion

In still air, an attractant plume disperses by molecular diffusion, which is described by the mass-balance equation (Veigele and Head, 1978):

$$q = \left(\frac{\partial}{\partial t} - D \nabla^2 \right) c, \quad (\text{II.1})$$

Where: q is the rate of emission per unit volume, with units of $\text{g sec}^{-1} \text{ cm}^{-3}$;
 D is the diffusion coefficient, $\text{cm}^2 \text{ sec}^{-1}$;
 c is the attractant concentration, g cm^{-3} ;
 $\frac{\partial}{\partial t}$ represents differentiation with respect to time;
 ∇^2 represents the Laplacian differential operator (Protter and Morrey, 1966; p. 567).

Theoretically Eq. II.1 has many solutions, depending on the initial concentration distribution and the first partial derivative, $\partial C / \partial r$, at all boundary surfaces. For heuristic purposes it is convenient to assume that the source is surrounded by a single boundary surface and the initial ($t = 0$) concentration is zero everywhere inside the boundary. The value of $\partial C / \partial r$ at this boundary is (Chamberlain, 1953; Judeikis and Stewart, 1976; Draxler and Elliot, 1977):

$$\frac{\partial C}{\partial r} = \frac{V_d}{D} C, \quad (\text{II.2})$$

Where: V_d is an empirical parameter, the deposition velocity, cm sec^{-1} .

The solution to Eqs. II.1-2 for dispersal inside a spherical boundary is (Carslaw and Jaeger, 1967, p. 367, and Appendix):

$$C = \frac{Q}{2\pi arD} \sum_{n=1}^{\infty} \frac{(ah-1)^2 + a^2 \theta_n^2}{a^2 \theta_n^2 + ah(ah-1)} [\sin(r\theta_n)/\theta_n] [1 - \exp(-D\theta_n^2 t)], \quad (\text{II.3})$$

Where: Q is the emission rate of the source, g sec^{-1} ;
 a is the radial distance of the boundary sphere, from the source cm;
 r is the radial distance of the measurement position from the source, cm;

t is the duration of emission, sec;
 h is the ratio V_d/D , cm^{-1} ;
 θ_n is the nth positive root of the equation
 $a \cot(a\theta) + ah = 1$. (II.4)

Equations II.3-4 are not restricted particularly to attraction problems with spherical boundaries because most attractants have values of D and V_d that fall within fairly narrow ranges, limiting the extent of boundary effects. The molecular diffusion coefficient of a sex pheromone is about $0.05 \text{ cm}^2/\text{sec}$ (Wilson et al., 1969; Hirooka and Suwanai, 1976), and most other attractants have molecular diffusion coefficients near $0.03-0.07 \text{ cm}^2/\text{sec}$ (Monchick and Mason, 1961; Lugg, 1968). However, unless conditions are strictly controlled, air currents usually occur that effectively increase D to $0.1-0.5 \text{ cm}^2/\text{sec}$ (Bossert and Wilson, 1963). The magnitude of the deposition velocity depends primarily upon the forces causing adsorption of the attractant vapor to the substrate. Interfaces composed of different vapors and different substrates have similar deposition velocities inasmuch as the vapor-substrate interactive forces are similar (Judeikis and Stewart, 1976). Measurements of deposition velocity typically vary over the range 0.1 to 10 cm/sec for Iodine-plastic, SO_2 -concrete, and pheromone-vegetation interfaces (Chamberlain, 1953, 1966; Judeikis and Stewart, 1976; Nakamura and Kawasaki, 1977). The following analysis

of Eqs. II.3-4 shows that, when D and V_d fall within the ranges given above, the effect of a boundary on the attractant distribution is usually small.

The spatial variation of the relative concentration, $C_r = C/Q$, is depicted in Figs. 3-6 at several different values of a , D , V_d , and t . The curves were calculated from the first 700 terms of the series in Eq. II.3, which converged after about 200 terms except at small r and t . The curve for $a = \infty$ corresponds to the boundless case, previously discussed by Bossert and Wilson (1963), whose solution reduces to:

$$C_r = \frac{Q}{2\pi Dr} \operatorname{erfc}(r/(4Dt)^{1/2}), \quad (\text{II.5})$$

Where: erfc is the complimentary error function (Carslaw and Jaeger, 1967).

Inspection of Figs. 3-4 shows that the smaller the boundary radius the smaller the variation of C_r with time, and as t increases the difference between C_r in a bounded and a boundless environment decreases. The 2 curves for $a = \infty$ differ considerably from each other, but the curve for $a = 150$ at $t = 60$ sec is quite similar to the curve for $a = 100$ at $t = 8.6 \times 10^5$ sec. After about 10^3 sec, there is very little difference between the curves $a = \infty$, $a = 1000$, and $a = 100$, short distances away from the respective boundaries. The curves for 10^3 sec are not plotted because they

Figure 3. Spatial variation of the relative concentration, $C_r = C/Q$, at $t = 60$ sec. The regression lines are calculated from Eqs. II.3-4 with $D = 1 \text{ cm}^2/\text{sec}$, and $V_d = 1 \text{ cm/sec}$. The radius of the boundary sphere, a , has units of cm.

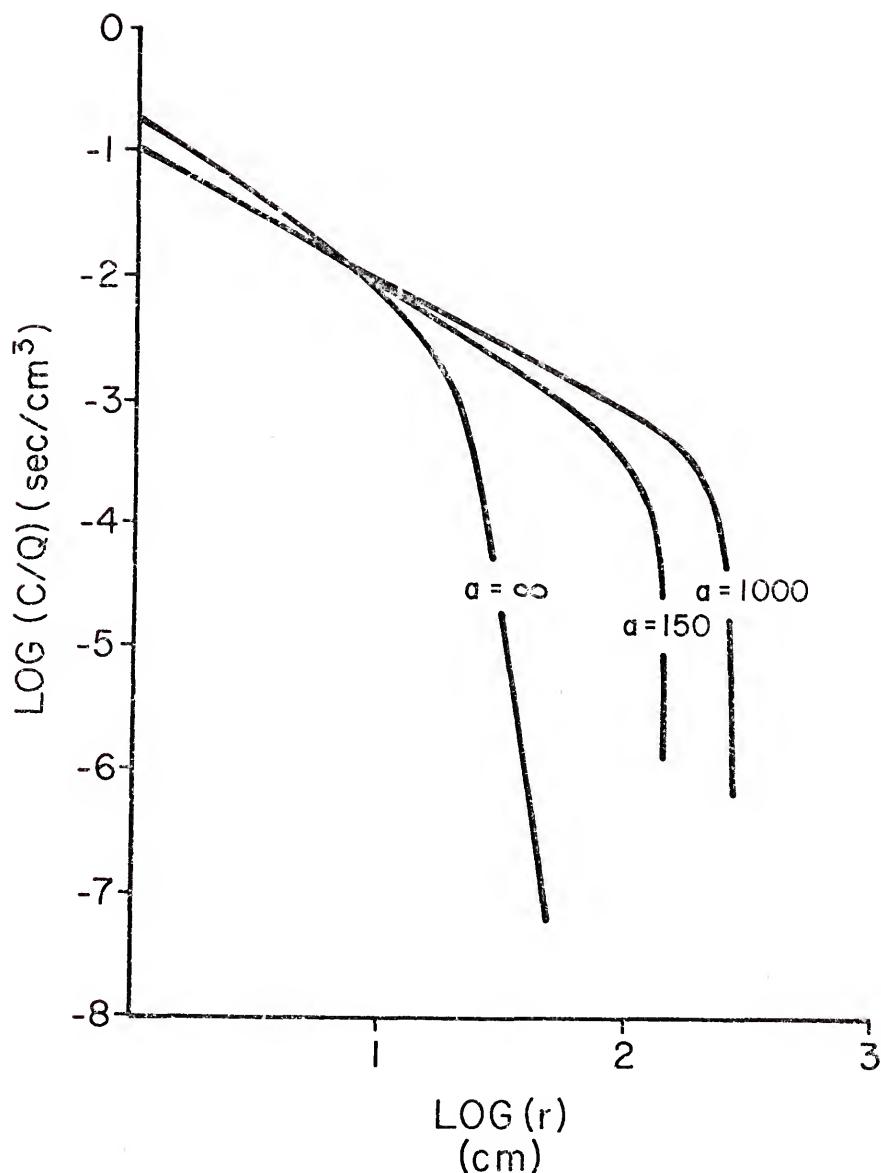


Figure 4. Spatial variation of the relative concentration, $C_r = C/Q$ at $t = 8.6 \times 10^5$ sec. The regression lines are calculated from Eqs. II.3-4 with $D = 1 \text{ cm}^2/\text{sec}$, and $V_d = 1 \text{ cm/sec}$. The radius of the boundary sphere, a , has units of cm.

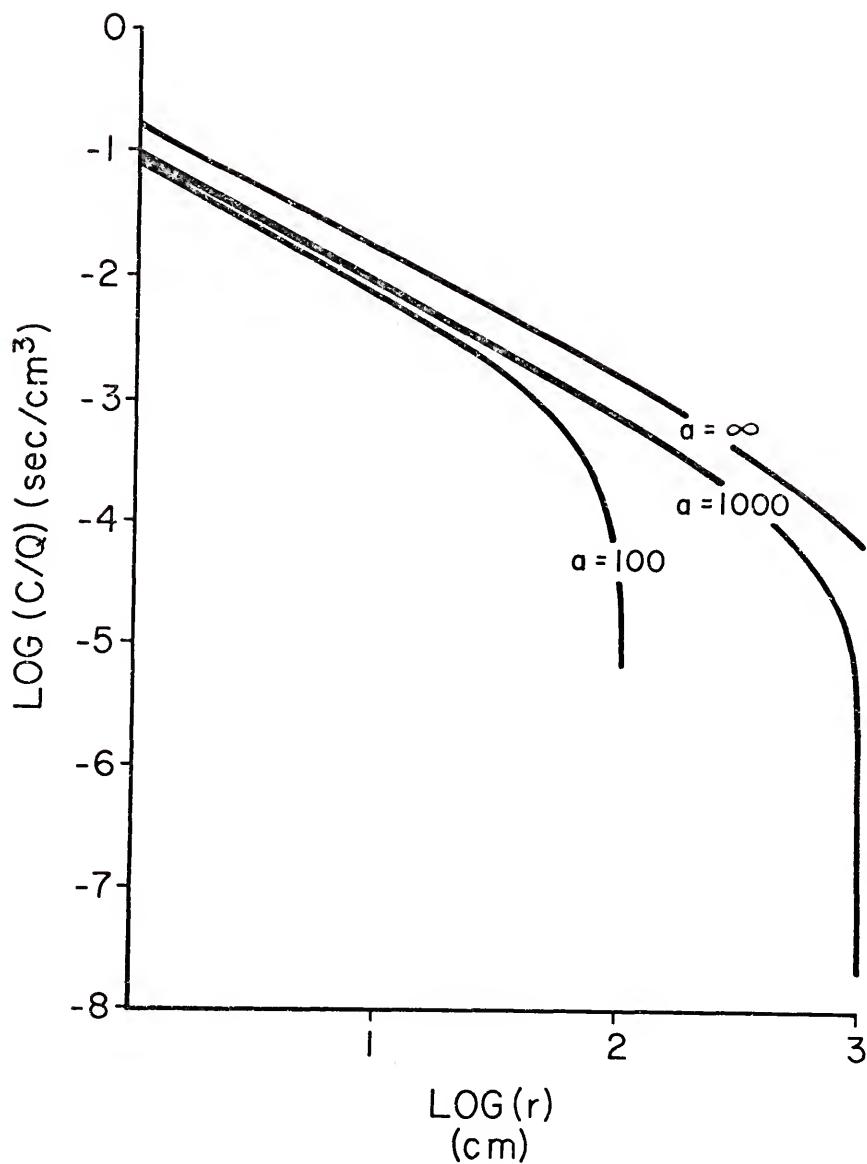


Figure 5. Variation of the relative concentration, $C = C/Q$, with respect to the diffusion coefficient D . The regression lines are calculated from Eqs. II.3-4 with $t = 8.6 \times 10^5$ sec, $V_d = 1$ cm/sec, and $a = 1000$ cm. D has units of cm^2/sec .

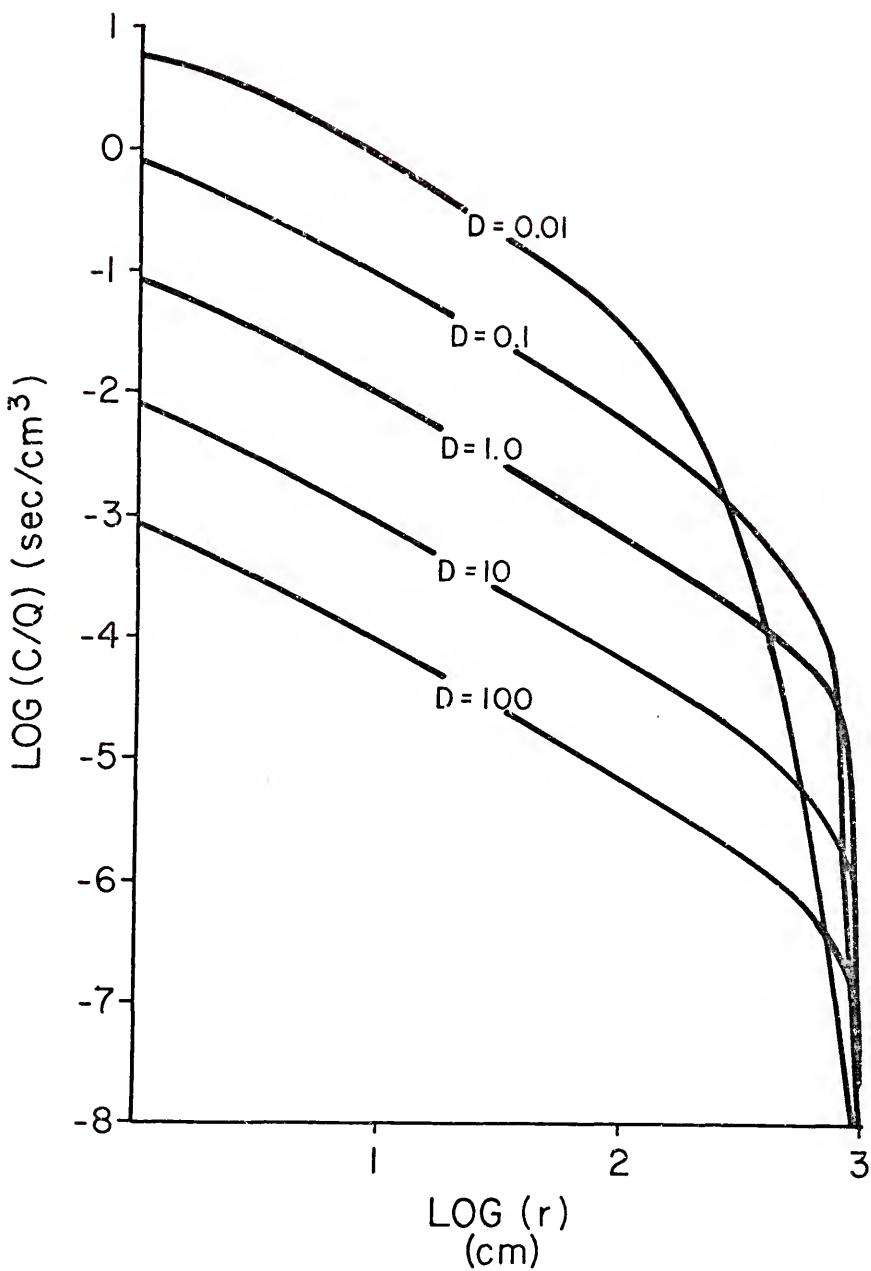
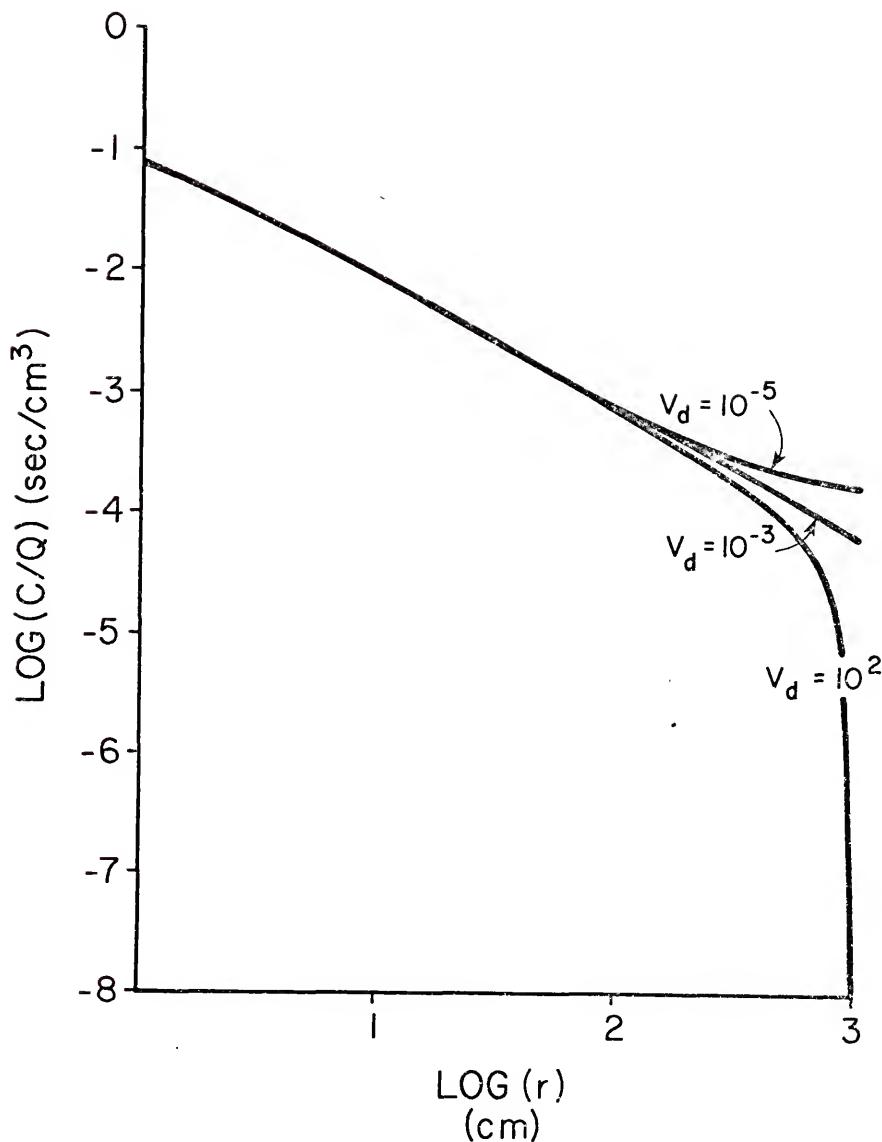


Figure 6. Variation of the relative concentration, $C_f = C/Q$, with respect to the deposition velocity, V_d . The regression lines are calculated from Eqs. II.3-4 with $t = 8.6 \times 10^5$ sec, $D = 1 \text{ cm}^2/\text{sec}$, and $a = 1000 \text{ cm}$. V_d has units of cm/sec .



are quite similar to the curves in Fig. 4. Indeed, the effect of the boundary can be disregarded so long as $r/a < 0.9$, unless D is considerably smaller than $1 \text{ cm}^2/\text{sec}$. This is shown in Figs. 5-6, where D ranges from 10^{-2} to $10^2 \text{ cm}^2/\text{sec}$, and V_d from 10^{-5} to 10^2 cm/sec , at $t = 8.6 \times 10^5 \text{ sec}$ and $a = 1000 \text{ cm}$. Even at the hypothetical lower limit of the molecular diffusion coefficient, $0.1 \text{ cm}^2/\text{sec}$, the influence of the boundary is negligible until $r/a > 0.75$. Under these conditions, the exact geometry of a boundary is unimportant, and the solution to Eqs. II.1-2 under any boundary geometry is similar to Eqs. II.3-4. This justifies the general use of Eqs. II.3-4 in a model for attraction in still air, provided that the results are interpreted with caution and when the emission duration is less than about an hour and/or $r/a > 0.9$.

Case II: Dispersal in Airflow of Zero Average Velocity

The next step of the derivation is to consider the effect of random air currents on the diffusion process. In most applications of a model the air has some movement. Often, random fluctuations of speed and direction occur, caused by superimposed whirls or eddies of various sizes. Eddies with a diameter greater than about 100 cm or less than about 5 cm have little effect on an attractant plume but eddies of intermediate diameter cause the plume to disperse rapidly (Aylor, 1976).

This kind of dispersal, called turbulent or eddy diffusion, is analogous to molecular diffusion. If the airflow has a near-zero average velocity, eddy diffusion is described via Eq. II.1, replacing the molecular diffusion coefficient with the sum of the molecular and eddy diffusion coefficients. The eddy diffusion coefficient of a vapor or an aerosol is $0.1\text{-}10 \text{ cm}^2/\text{sec}$ in a calm environment (Sutton, 1953; Pasquill, 1961; Bossert and Wilson, 1963; Allen, 1975). Just as in molecular diffusion, Eqs. II.3-4 can be used as a general solution to the turbulent diffusion problem, provided that the results are interpreted with caution when $t < 3600 \text{ sec}$ and/or $r/a > 0.9$.

Case III: Dispersal in Airflow of
Constant Average Velocity

The derivation of an attraction model is now completed by considering the effect of relatively stable convection on molecular and turbulent diffusion processes. An exact mathematical description of convective-diffusive dispersal does not exist, but many time-averaged statistical descriptions have been published (e.g., Sutton, 1953; Pasquill, 1961; Lamb et al., 1975). The Sutton equation is:

$$C = \frac{2Q}{K_y K_z v x^{1.75}} \exp \left[-x^{1.75} \left(\frac{y^2}{K_y^2} + \frac{z^2}{K_z^2} \right) \right], \quad (\text{II.6})$$

where: C is the attractant concentration, with units of g sec^{-1} ;
 Q is the attractant's emission rate, g sec^{-1} ;
 v is the mean air velocity, cm sec^{-1} ;
 X is the distance from the source along the airflow axis, cm ;
 Y is the distance from the source along cross-wind horizontal axis, cm ;
 Z is the distance from the source along the vertical axis, cm ;
 K_y, K_z are empirical constants whose values have been tabulated for different turbulence levels, $\text{cm}^{0.125}$ (Gifford, 1960).

Equation II.6 has been incorporated into several of the models cited in the introduction.

However, there are several cautions to using Eq. II.6. When barriers or thermal stratification interfere with free air movement, or the airflow becomes highly unstable, tabulated values of K_y and K_z are not very reliable (Sutton, 1953). Under such conditions, the dispersal pattern can be observed directly by using smoke plumes, and the tabulated values of K_y and K_z can be replaced with values determined by the extent of the plumes (Pasquill, 1961). Even allowing for these effects, Eq. II.6 provides no information about the instantaneous concentration distribution, which is a more important determinant of the insect's searching behavior

than the average distribution (Aylor, 1976). Qualitative effects of differences in the instantaneous distribution can nevertheless be incorporated into the model as follows.

An attractant plume typically consists of 3 distinct regions that differ in shape (Aylor, 1976; J. Kittredge, personal communication). Region I extends 0.5-10 m downwind of the source. The plume in this region is a single filament whose width is smaller than the widths of the smallest eddies; thus, it disperses solely by the slow process of molecular diffusion. It splits into several filaments in Region II, which extends from the edge of Region I to about 50-70 m downwind, depending on the turbulence and the air velocity (Hinze, 1975). In addition, it begins to expand rapidly because its width is now comparable to the widths of the smaller eddies, allowing dispersal by turbulent diffusion. This expansion continues until the limits of the plume become indistinct in the final region, which extends downwind indefinitely from the edge of region II. The plume has greater definition in region I than in region II, and the least definition in region III.

The regional differences in plume shape can be used to improve the model's estimates of the attraction space. According to current theories of flight orientation behavior (Farkas and Shorey, 1974; Kennedy, 1974; and references therein), an insect finds it easier to steer toward a source when the plume structure is well-defined. A model incorporating this hypothesis predicts that an insect is more likely

to reach the source if it enters region I than if it enters the other 2 regions. A corollary is that the smaller the dimensions of the source, the greater the extent of region I, and the greater the probability of an insect finding the source.

The choice whether to use Eq. II.6 or Eqs. II.3-4 in a particular application of the model depends upon the turbulence level, the obstructing boundaries, and the shape of the plume. If the shape of the plume is unknown, it can be determined by smoke plume observations (see Chapter I). Generally Case I dispersal, characterized by the absence of turbulence, occurs only in a highly controlled environment. If a plume in turbulent air is nearly spherical, Case II applies, and if it is ellipsoidal, Case III applies. The movement of a plume in sheltered areas, cul-de-sacs, or a closed, empty warehouse with an isothermal temperature distribution usually fits a Case II dispersal pattern, while Case III dispersal is more likely to occur in open ventilated corridors or highly stratified air.

Before proceeding with applications of the model it is appropriate to consider briefly the validity of Assumptions 1-4 and the precision of the dispersal equations. The simplified problem obtained by adopting these assumptions neglects such behavioral factors as visual attraction (Shorey and Gaston, 1965; Hienton, 1974), anemotaxis (Kennedy, 1974), habituation (Thompson and Spencer, 1966; Traynier, 1968;

Sower et al., 1973; Marks, 1978) and changes in the intensity of a response at different attractant concentrations (Cain and Engen, 1969; Mayer, 1973; Bartell and Lawrence, 1977). None of these factors are quantified very precisely; consequently, their inclusion in the model would not necessarily improve its precision at this time. The model also neglects such physical factors as pheromonal lability (Lundberg, 1961; Sower et al., 1975) differences in the ratios of attractant components (Roelofs, 1978), and changes in the emission rate of the source at different temperatures and airflows. These factors, as well as the statistical nature of atmospheric mass-transfer processes, limit the precision of the dispersal equations used in the model. Because of these limitations, the model must be used in conjunction with, rather than instead of experimental studies. Notwithstanding, the model provides considerable insight into the attraction process, as shown by the following applications.

Results

The applications presented here are concerned primarily with Case II dispersal because Case I is of little practical interest and Case III has been treated in detail by the models cited earlier. Under Case I dispersal, the model treats the hypothesis (Traynier, 1968; Perez and Hensley, 1973) that pheromone-laden air tends to sink. Under Case II, attraction spaces and altered-behavior spaces are calculated

for calling insects and sex pheromone traps. The model also deals with attraction to competing sources. Under Case III, the model entertains the possibility that insects can be attracted from outside a warehouse.

Case I Dispersal: Effect of Gravity on Pheromone in Still Air

Equations II.1, 3, and 4 do not consider gravitation; thus, by default they predict that the dispersal of pheromone in still air is unaffected by the high molecular weight of pheromone molecules relative to the weight of air molecules. It will now be shown that this prediction remains unchanged after gravitation is incorporated into the model.

The effect of gravity is determined by Archimedes' principle (Sears, 1958, p. 365), in that an air-pheromone mixture is subject to a gravitational force proportional to the difference between the density of the mixture and the density of the air surrounding it. The standard density of air is $\rho_a = 1.3 \times 10^{-3} \text{ g/cm}^3$ (Sears, 1958). The density of the air-pheromone mixture is, by definition:

$$\rho_{ap} = \frac{m_a}{V} + \frac{m_p}{V} \quad (\text{II.7})$$

Where: m_a is the mass of air inside V, g;
 m_p is the mass of pheromone inside V, g;
 V is the volume, cm^3 .

The pheromone vapor density, m_p/V , reaches a maximum at partial pressures approaching the vapor pressure, the pressure exerted by the pheromone vapor when the air is saturated. The vapor pressure and the corresponding saturated vapor density of a 12-16 carbon sex pheromone are about 1×10^{-4} cm-Hg and 10 ng/cm^3 , respectively (Hirooka and Suwanai, 1976). The magnitude of m_a/V in Eq. II.7 can be calculated by combining Dalton's Law of Partial Pressures, the Ideal Gas Law, and the relationship between mass and molecular weight which are respectively,

$$P_{at} = P_p + P_a, \quad (\text{II.8})$$

$$PV = NRT, \quad (\text{II.9})$$

and

$$m = NM, \quad (\text{II.10})$$

Where: P is the pressure in units of cm Hg or dyne cm^{-2} ;
 N is the number of moles;
 R is the gas constant, 8.31×10^7 ergs mole^{-1} Kelvin;
 T is the temperature, deg Kelvin;
 m is the mass, g;
 M is the molecular weight, g/mole.

The subscripts a, p, and at, refer to unadulterated air, pheromone, and atmosphere, respectively. The result of combining Eqs. II.8-10 is

$$\frac{m_a}{V} = \rho_a - \frac{m_p M_a}{V M_p}. \quad (\text{II.11})$$

Accordingly, Eq. II.7 can be rewritten:

$$\rho_{ap} = \rho_a + \frac{m_p (1 - M_a/M_p)}{V}. \quad (\text{II.12})$$

M_a , the molecular weight of air, is about 29 g/mole and M_p , the molecular weight of the pheromone, is about 225 g/mole. Given a maximum value of 10 ng/cm^3 for m_p/V , the maximum density of the air-pheromone mixture is:

$$\rho_{ap} = 1.3 \times 10^{-3} + 8.7 \times 10^{-9} \text{ g/cm}^3. \quad (\text{II.13})$$

This shows that there is essentially no difference between the density of the air-pheromone mixture and the unadulterated air; so by Archimedes' principle, gravity has little effect on the mixture.

By contrast, a solvent such as diethyl ether may sink in still air because it has a high vapor pressure, about 442 mm-Hg. Using Eq. II.9 and the conversion factor $1 \text{ cm-Hg} = 1.33 \times 10^4 \text{ dynes/cm}$,

$$\frac{m_e}{V} = \frac{M_p}{RT} = 1.75 \times 10^{-3} \text{ g/cm}^3, \quad (\text{II.14})$$

where: M_p is the molecular weight of diethyl ether,
74 g/mole;
 m_e is the mass of ether inside V, g.

Accordingly, the density of the air-diethyl ether mixture
is $\rho_{ae} = 2.36 \times 10^{-3} \text{ g/cm}^3$.

The net force on 1 ml of ether-saturated air is, by
Archimedes' principle:

$$F = (\rho_{ae} - \rho_a) 980 \text{ cm}^4/\text{sec}^2 = 1.04 \text{ dynes.} \quad (\text{II.15})$$

After 1 sec a ml of ether-saturated air falls at the
velocity

$$V = \frac{F}{\rho_{ae} \times 1 \text{ ml}} (1 \text{ sec}) = 440.7 \text{ cm/sec.} \quad (\text{II.16})$$

This is about half the rate of fall of a solid object. However, immediately after the mixture is emitted it begins to disperse into the air. Within a short period of time the density inside V equilibrates with that of the surrounding air and the rate of fall decreases to zero.

Case II Dispersal: Attraction and Altered Behavior Spaces of IMM

If the attraction and altered-behavior thresholds of an insect are known, Figs. 3 and 4 provide estimates of the attraction and altered-behavior spaces of an attractant source in a Case II environment. The insect considered here is the widespread postharvest pest, P. interpunctella (IMM). A male IMM has an upwind anemotactic threshold of 6.8×10^{-9} ng/cm³ (1.0^{-17} molar) at 34°C, 5.6×10^{-7} ng/cm³ at 23°C, and it has a hypothetical altered-behavior threshold of about 10^{-5} ng/cm³ (see Chapter I). A calling virgin female IMM emits pheromone at 8×10^{-4} ng/sec (Sower and Fish, 1975), and typical sex pheromone traps for capturing IMM emit 0.01-0.76 ng/sec (Vick et al., 1979). The relative thresholds for each emission rate and temperature are given in Table 3. Insertion of the IMM female's relative attraction threshold into Fig. 3 demonstrates that the attraction space of a female after one min of calling is rather insensitive to temperature but somewhat dependent on boundary position. The entire volume inside a boundary of 150 cm radius is an attraction space. The attraction space inside a boundary of 1000 cm radius is a sphere of about 250 cm radius. In a boundless environment, the attraction sphere has a radius of about 40 cm. Actually, there is little practical difference among these radii. The spaces calculated by the model for the IMM are compared with

Table 3. Relative attraction thresholds, $C_r = C/Q$, and relative altered-behavior thresholds, C_{rd} , for a female IMM and 2 sex pheromone traps emitting at different rates. Units of C_r and C_{rd} are sec/cm³.

Parameter	Female IMM	Pheromone trap	Pheromone trap
Q (ng/sec)	8×10^{-4}	0.01	0.76
C_r at 23°C	7×10^{-4}	5.6×10^{-5}	7.4×10^{-7}
34°C	8.5×10^{-6}	6.8×10^{-7}	8.9×10^{-9}
C_{rd}	1.25×10^{-2}	10^{-3}	1.3×10^{-5}

the spaces for different insects in Table 4. The difference between the first 2 estimates, derived from Eq. II.1, and the last 2 estimates, derived from Eq. II.6, indicates primarily the effect of convection on the pheromone dispersal pattern.

Hitherto, the concept of an altered-behavior space has been applied to traps but not to calling insects, perhaps because it had been assumed that the concentration around a calling insect does not rise above the altered-behavior threshold. According to the model however, calling females of both IMM and Trichoplusia ni (Hubner) species are surrounded by altered behavior spaces of small but definite extent. Using Table 3 and Fig. 3, the altered-behavior threshold of a female IMM occurs at about 6 cm. A female Trichoplusia ni (Hubner) emits pheromone at the rate of 0.1 ng/sec, and a male has an activation threshold of about 3×10^{-7} ng/cm³ (Sower et al., 1971). If it is assumed that the altered behavior threshold is 10^{-4} ng/cm³, 3 orders of magnitude above the activation threshold (Roelofs, 1978), the relative threshold is $C_{rd} = 10^{-3}$ sec/cm³, and from Fig. 3, the altered-behavior space is a sphere of about 15-60 cm radius.

The attraction and altered-behavior spaces of IMM sex pheromone traps can be determined using Table 3 and Fig. 4. If either trap in Table 3 is the source, essentially the entire volume inside a boundary of 10 or 1000 cm radius is

Table 4. Calculated values for the maximal communication distance or attractive range of an insect, using either Eqs. II.3-4 or Eq. II.6.

Insect	Range (m)	Reference
<u>Plodia interpunctella</u> (Hubner)	0.4-2.5	Chapter II
<u>Pogonomyrmex badius</u> (Latreille)	1.04	Bossert & Wilson (1963)
<u>Trogoderma glabrum</u> (Herbst)	0.8-10	Shapas (1977)
<u>Hyphantria cunea</u> (Drury)	3-10	Hirooka & Suwanai (1976)
<u>Spodoptera litura</u> (F.)	80	Nakamura & Kawasaki (1976)
<u>Trichoplusia ni</u> (Hubner)	1-100	Sower et al. (1971)

above the attraction threshold. At 0.76 ng/sec the entire volume is also above the altered-behavior threshold. By contrast, the 0.01 ng/sec trap has an altered-behavior sphere of 71 cm radius inside a 1000 cm boundary and 45 cm radius inside a 100 cm boundary. This suggests that a trap emitting 1 ng/sec might capture fewer IMM than an otherwise identical trap emitting 10^{-3} ng/sec.

Because the male IMM anemotactic threshold to sex pheromone is about 2 orders of magnitude higher at 23°C than at 34°C , it is surprising that there is little effect of temperature on the predicted attraction space of a calling female or a pheromone trap. This result is due to a rapid decrease in C_r with respect to position once C_r falls below about 10^{-4} sec/cm³. The temperature could have a large effect if the threshold C_r were higher than 10^{-4} sec/cm³. Such high threshold values of C_r may occur for non-pheromonal attractants.

The model cannot be used to calculate attraction to competing sources unless the attraction spaces are nonoverlapping or the principal searching mechanism is chemotaxis. If the insect searches by additional mechanisms, e.g. klinokinesis, chemokinesis or vision (Wright, 1958; Farkas and Shorey, 1974; Wall and Perry, 1978; Baker and Carde, 1979) the problem of attraction to competing sources becomes very complicated, particularly if trap-female competition is considered. For example, a female IMM generally calls from

walls, ceilings, or other exposed surfaces. Typically, a male IMM stimulated by sex pheromone orients visually to such surfaces, investigating objects resembling female IMM (Sower et al., 1975). This behavior increases the probability of locating a female but decreases the probability of capture by a trap unless the trap is highly attractive visually. Thus, as the density of female IMM increases, a trap could lose efficiency much more rapidly than the model would predict from comparisons of the attraction spaces.

However, if the attraction spaces are nonoverlapping or the principal searching mechanism is chemotaxis, attraction to competing sources can be calculated by superposition of individual solutions of the model equations. The procedure for nonoverlapping sources has been treated in detail elsewhere (Knippling and McGuire, 1966; Nakamura and Oyama, 1978), so only attraction under chemotaxis will be considered here. Suppose 2 sources, E₁ and E₂, are located 500 cm apart in a warehouse whose length-width-height dimensions are about 20 m each. If the emission rates of E₁ and E₂ are equal and the attraction spaces overlap, an insect inside the overlapping region will fly to the closest source. If the emission rates are unequal, the probability of attraction to either source can be predicted using Fig. 4, which indicates that a 10-fold decrease in pheromone concentration is roughly equivalent to a 10-fold increase in the

distance from the source. Accordingly, when the emission rate of E1 is 10-fold greater than that of E2, an insect inside the overlapping space flies to E1 unless it is within about 45 cm of E2.

Case III Dispersal: Attraction of Insects from Outside a Warehouse

Equations II.3-4 can be combined with Eq. II.6 to determine whether emission from a trap inside a warehouse produces an above-threshold concentration of pheromone outside. Suppose that a trap emitting IMM sex pheromone at the rate of 0.1 ng/sec is placed near the middle of a warehouse whose length-width-height dimensions are about 20 m each. After several days a 2 x 2 m door is opened. The ambient temperature is 27°C, and the outside airflow is a constant 50 cm/sec. The K_y and K_z in Eq. II.6 are assumed to have the values tabulated by Sutton (1953) for dispersal under stable conditions, 0.4 and $0.2 \text{ cm}^{0.125}$, respectively. The maximum rate of flow of pheromone through the door is (Judeikis and Stewart, 1976):

$$Q = (RT/2\pi M_p)^{1/2} C (4 \times 10^4 \text{ cm}^2). \quad (\text{II.17})$$

The values of R and M_p are given in the Results: Case I section. The concentration, C, is found by inspection of Fig. 4, which indicates that the pheromone concentration near the door is about 10^{-6} ng/cm^3 ($C_r = 10^{-5} \text{ sec/cm}^3$).

Inserting these values into Eq. II.17 gives $Q = 168 \text{ ng/sec}$. This rate decreases immediately after the door is opened, and continues to decrease to 0.1 ng/sec . For estimation purposes it is convenient to choose $Q = 10 \text{ ng/sec}$ and $Y = Z = 0$ in Eq. II.6, which then reduces to

$$C = 1.59 \times 10^{-9} \text{ g cm}^{-1.25} x^{-1.75}. \quad (\text{II.18})$$

The behavioral threshold of a male IMM is ca. 10^{-17} g/cm^3 (see Chapter I). Accordingly, the maximum downwind distance from which a male IMM can be attracted is

$$\begin{aligned} x &= (10^{-17} \text{ g cm}^{-3}/1.59 \times 10^{-9} \text{ g cm}^{-1.25}, -0.571 \\ &= 4.82 \times 10^4 \text{ cm}. \end{aligned} \quad (\text{II.19})$$

If the pheromone is emitted from a 1 cm^2 hole instead of a $2 \text{ m} \times 2 \text{ m}$ door, the emission rate is $Q = 4.2 \times 10^{-12} \text{ g/sec}$. At this rate Eq. II.6 reduces to

$$\begin{aligned} x &= (10^{-17} \text{ g cm}^{-3}/6.68 \times 10^{-13} \text{ g cm}^{-1.25}, -0.571 \\ &= 569 \text{ cm}. \end{aligned} \quad (\text{II.20})$$

Thus, the attraction of insects from outside the warehouse cannot be neglected unless the external openings are less than about 1 cm^2 area.

Discussion

Some of the predictions resulting from the incorporation of boundary effects, plume shape effects, altered-behavior thresholds, and gravitation into the attraction model warrant further discussion. These factors are considered in order below, in the context of previously published work.

Inclusion of boundary effects in the model results in 2 predictions. First, according to Figs. 3-4, the position of the boundary is important at short emission durations applicable to a calling insect, but not at long emission durations applicable to a trap. Second, near a typical boundary surface the attractant concentration is much lower than it would be without the boundary, although the concentration may remain at high levels if the deposition velocity is extremely low, e.g., 10^{-5} cm/sec in Fig. 6. Such a boundary would be considered a reflector rather than an adsorber. These predictions suggest that a flying insect is more likely to be stimulated by sex pheromone or other attractants than an insect sitting or walking on an adsorptive surface. Observations by Visser (1976) on the host-plant searching behavior of Leptinotarsa decemlineata Say support such a hypothesis. A corollary hypothesis is that a calling insect extending its pheromone gland away from the surface on which it is sitting has a larger attraction space than insect calling directly from the surface. The

former calling behavior occurs frequently in female IMM, Bombyx mori (L.), and several other insects (e.g., Hammack et al., 1976).

Consideration of plume shape effects in the Methods: Case III section, led to the hypothesis that well-defined plumes from attractant sources of small dimensions are more efficient in attracting insects than indistinct plumes from attractant sources of large dimensions. There are at least 2 experimental studies bearing in part on this hypothesis. Lewis and Macaulay (1976) found that traps emitting well-defined smoke plumes tended to capture more insects than those emitting indistinct smoke plumes. In a related study Macaulay and Lewis (1977) tested the effect of source dimensions on trap catches with inconclusive results. However, there are objections to the methodology of the 2nd study, in that the large-sized sources had 10-fold to 100-fold greater emission rates than the small-sized sources. Because the resulting attraction spaces of the large-sized sources were much larger than the spaces of the small-sized sources, the attraction efficiencies cannot be compared directly and further study is needed to confirm or deny the hypothesized plume shape effect.

The altered-behavior spaces predicted by the model are of theoretical use, not only for explaining decreases in trap catches with increases in emission rate, but also for suggesting the function of the altered-behavior threshold.

This is illustrated by the calculations in the Results:

Case II section, for the altered-behavior spaces of IMM sex pheromone traps and calling females. Because the entire volume inside a 100 or 1000 cm active space of a trap emitting 0.1 ng/sec was an altered-behavior space, it was proposed that a trap emitting 10^{-3} ng/sec might have a greater efficiency in a warehouse than a trap emitting 1 ng/sec. Such an effect has not been observed with IMM, but Vick et al. (1979) reported a similar effect in trapping studies of Sitotroga cerealella (Olivier). In a 6.1 x 6.1 x 2 m room, traps emitting S. cerealella sex pheromone at 0.02 ng/sec captured more males than traps emitting 0.2 ng/sec.

The finding that calling females of both IMM and T. ni emit pheromone at rates sufficient to create small altered-behavior spaces suggests a function for the altered-behavior threshold. Under Case II dispersal the threshold occurs about 6 cm away from an IMM female and 60 cm from a T. ni female. The corresponding distances can also be calculated for Case III dispersal using Eq. II.6. In a relatively calm airflow of 50 cm/sec, the altered-behavior threshold occurs about 4 cm downwind from an IMM female and 18 cm downwind from a T. ni female, using $K_y K_z = 0.08 \text{ cm}^{0.25}$, $C_{rd} = 1.25 \times 10^{-2} \text{ sec/cm}^3$ for IMM and $C_{rd} = 10^{-3} \text{ sec/cm}^3$ for T. ni. The existence of this threshold may increase the probability of a stimulated insect finding a calling

insect because it alters the searching behavior from an extensive search pattern to a more intensive search pattern (Roelofs, 1978). The limited range for the altered-behavior spaces of the 2 insects supports this hypothesis.

It remains to discuss hypotheses explaining why searching insects tend to approach calling insects or traps from below in still or nearly still air (Traynier, 1968; Killiner and Ost, 1971; Murliss and Bettany, 1977). The usual hypothesis is that pheromone falls in still air, but this is shown to be invalid in the Results: Case I section. One alternative hypothesis is that the presence of a reflective boundary below the source could result in a greater concentration of pheromone just above the boundary surface than at positions some distance above the plume axis. Inspection of Figs. 3, 4, and 6 indicates that this could happen if both V_d and t are small. Another hypothesis is that the turbulence level tends to be proportional to height above ground; thus, the plume may be more well-defined and easier to follow near the ground than at greater heights. However, neither hypothesis explains why an insect would approach the trap from below in low airspeeds but not in high airspeeds. It is also possible that the behavior is relatively independent of the actual pheromone distribution. Further study is necessary to resolve these questions.

Considerations of predictions based on the model leads to the following hypotheses for optimizing sex pheromone

trap design and placement: (1) Sources of small dimensions produce more well-defined plumes for longer distances than sources of large dimensions. Thus, trap catches could be improved by reducing the dimensions of the source. (2) If the insect has an altered-behavior threshold, a trap emitting a high rate and producing an above-threshold concentrations could capture fewer insects than a trap with a low emission rate. Thus, an experimental design using a large number of traps with small active spaces may be a more effective monitor of the pest population than a design using a small number of traps with large active spaces. A side benefit of the former design is that it mitigates the effects of temperature inversion and barriers on pheromonal distribution. (3) If there are openings greater than about 1 cm^2 in a warehouse, pheromone sources inside can attract pests from outside the warehouse. Warehouse pest monitoring experiments should be designed to account for this effect.

CONCLUSIONS

A model of insect attraction to odorant sources was derived, unique in its treatment of adsorptive boundaries obstructing odorant flow. The generality and versatility of the model was demonstrated by considering the attraction of several different insects to sex pheromone sources in warehouse, field, and still-air environments. Because the important relationships of the model are presented graphically as well as mathematically, and because pheromonal behavioral thresholds generally range between 10^2 and 10^6 molecules/cm³, the procedure for estimating attraction of other insects to sex pheromone sources is manifest. Calculations of the model resulted in testable, experimentally supported hypotheses regarding optimal trap designs, and the effects of different parameters on the odorant concentration distribution. Further improvement in the precision of the model requires a better understanding of searching behavior, rather than a more precise quantitation of odorant dispersal. These considerations lead to the following conclusions: (1) The model can be applied to a wider range of attraction problems than previous models, which increases its usefulness for pest management studies and theoretical analyses of the attraction process. (2) It offers new insights into improving techniques for monitoring insect

pest populations. (3) Future experimental and theoretical studies of insect attraction should be directed more toward increasing the quantitative and qualitative understanding of searching behavior and less toward refining calculations of the odorant concentration distribution.

APPENDIX
DERIVATION OF EQUATION II.3

Because the mathematics of thermal and mass diffusion are equivalent, Eq. II.3 can be derived from the heat-transfer equation for a unit instantaneous heat source (Carslaw and Jaeger, 1959, p. 367):

$$T = \frac{1}{2\pi ar} \sum_{n=1}^{\infty} \frac{(ah'-1)^2 + a^2 \theta_n^2}{a^2 \theta_n^2 + ah'(ah'-1)} \quad (A.1)$$

$$\sin(r\theta_n) \sin(r'\theta_n) \exp(-\kappa \theta_n^2 t),$$

- Where:
- T is the temperature, deg C;
 - a is the boundary radius, cm;
 - r is the radius at which the temperature is calculated, cm;
 - r' is the radius of the source, cm;
 - h' is the ratio H/K, cm^{-1} ;
 - H is the coefficient of surface heat transfer, $\text{cal cm}^{-2} \text{sec}^{-2} \text{sec}^{-1} \text{deg}^{-1} \text{C}$;
 - K is the thermal conductivity, $\text{cal sec}^{-1} \text{cm}^{-1} \text{deg}^{-1} \text{C}$;
 - κ is the thermometric conductivity, $\text{cm}^2 \text{sec}^{-1}$;
 - θ_n is the nth positive root of the equation $a \cot(a\theta) + (ah'-1) = 0$. (A.2)

The boundary conditions specify that $0 \leq r < a$. There is a unit instantaneous source at $r = r'$. Heat transfer at a is governed by the equation

$$\phi = HT, \quad (A.3)$$

where: ϕ is the flux, the number of calories transferred across a 1 cm² surface in 1 sec (Carslaw and Jaeger, 1967, p. 19).

The heat diffusion equation can be transformed to a mass diffusion equation by replacing T with C, κ with D, and H with v_d (Carslaw and Jaeger, 1967, p. 28):

$$C = \frac{1}{2\pi ar}, \sum_{n=1}^{\infty} \frac{(ah-1)^2 + a^2 \theta_n^2}{a^2 \theta_n^2 + ah(ah-1)} [\sin(r\theta_n) \sin(r'\theta_n) \exp(-D\theta_n^2 t)], \quad (A.4)$$

where: h is the ratio, v_d/D , cm⁻¹.

To convert from a diffusion equation for a unit instantaneous source to the equation for a source emitting at the constant rate, Q, Eq. A.4 must be integrated over the measurement period. It is also convenient to use the approximation:

$$\frac{\sin(r'\theta_n)}{r'\theta_n} = 1, \quad (A.5)$$

which is valid for $r' \ll a$. Accordingly,

$$C = \frac{Q}{2\pi ar} \sum_{n=1}^{\infty} \frac{(ah-1)^2 + a^2 \theta_n^2}{a^2 \theta_n^2 + ah(ah-1)} (\theta_n) \sin(r\theta_n) \\ \int_0^t \exp[-D\theta_n^2(t-t')] dt', \quad (A.6)$$

which gives Eq. II.3 in the text:

$$C = \frac{Q}{2\pi arD} \sum_{n=1}^{\infty} \frac{(ah-1)^2 + a^2 \theta_n^2}{a^2 \theta_n^2 + ah(ah-1)} \quad (A.7)$$

$$[\sin(r\theta_n)/\theta_n][1 - \exp(-D\theta_n^2 t)].$$

REFERENCES

- ABBOT, W. S. 1925. A method of computing the effectiveness of an insecticide. J. Econ. Entomol. 18:265-267.
- ALLEN, L. H., JR. 1975. Line-source carbon dioxide release III. Predictions by a two-dimensional numerical diffusion model. Boundary-Layer Meteorol. 8:39-79.
- AYLOR, D. E. 1976. Estimating peak concentration of pheromones in the forest. pp. 177-188, in J. E. Anderson and H. K. Kaya (eds). Perspectives In Forest Entomology. Academic Press, New York.
- AYLOR, D. E., PARLANGE, JEAN-YVES, and GRANETT, J. 1976. Turbulent dispersion of Disparlure in the forest and male gypsy moth response. Environ. Entomol. 5: 1026-1032.
- BAKER, T. C., and CARDE, R. T. 1979. Courtship behavior of the Oriental fruit moth (Grapholitha molesta): experimental analysis and consideration of the role of sexual selection in the evaluation of courtship pheromones in the Lepidoptera. Ann. Entomol. Soc. Am. 72:173-188.
- BARAK, A., and BURKHOLDER, W. E. 1976. Trapping studies with Dermestid sex pheromones. Environ. Entomol. 5: 111-114.
- BARTELL, R. J., and LAWRENCE, L. A. 1977. Reduction in responsiveness of male apple moths, Epiphyas postvittana, to sex pheromone following pulsed pheromonal exposure. Physiol. Entomol. 2:1-6.
- BOSSERT, W. H. 1968. Temporal patterning in olfactory communication. J. Theoret. Biol. 18:157-170.
- BOSSERT, W. H., and WILSON, E. O. 1963. The analysis of olfactory communication among animals. J. Theoret. Biol. 5:443-469.
- BOX, G. E. P., HUNTER, W. G., and HUNTER, J. S. 1978. Statistics for Experimenters. John Wiley & Sons, New York.

- BROWNLEE, R. G., and SILVERSTEIN, R. M. 1968. A micro-preparative gas chromatograph and a modified carbon skeleton determinator. Anal. Chem. 40:2077-2079.
- BURSELL, E. 1964. Environmental aspects: Temperature, pp. 284-317, in Rockstein, M. (ed.). The Physiology of Insecta. Academic Press, New York.
- CAIN, W. S., and ENGEN, T. 1969. Olfactory adaptation and the scaling of odor intensity. pp. 127-141, in C. Pfaffmann (ed.). Olfaction and Taste III. Rockefeller Univ. Press, New York.
- CARSLAW, H. S., and JAEGER, J. C. 1967. Conduction of Heat in Solids. Oxford Univ. Press, London.
- CHAMBERLAIN, A. C. 1953. Experiments on the deposition of Iodine 131 vapor onto surfaces. Phil. Mag. 44:1145-1153.
- CHAMBERLAIN, A. C. 1966. Transport of gases to and from grass and grass-like surfaces. Proc. Roy. Soc. (Lond.) A 290:236-265.
- COSTER, J. E., PAYNE, T. L., EDSON, L. J., and HART, E. R. 1978. Influences of weather on mass aggregation of southern pine beetles at attractive host trees. Southwest Entomol. 3:14-20.
- DRAXLER, R. P., and ELLIOT, W. P. 1977. Long-range travel of airborne material subjected to dry deposition. Atmos. Environ. II:35-40.
- FARKAS, S. R., and SHOREY, H. H. 1974. Mechanisms of orientation to a distant pheromone source, pp. 81-95 in M. C. Birch (ed.). Frontiers of Biology 32. American Elsevier Publ. Co., New York.
- FINNEY, D. J. 1971. Probit Analysis. Cambridge University Press, Cambridge.
- FUYAMA, Y. 1976. Behavioral genetics of olfactory responses in Drosophila I. Olfactometry and strain differences in Drosophila melanogaster. Behav. Genetics 6:407-420.
- GASTON, L. K., SHOREY, H. H., and SAARIO, C. A. 1971. Sex pheromones of noctuid moths. Rate of evaporation of a model compound of Trichoplusia ni sex pheromone from different substrates at various temperatures and its application to insect orientation. Ann. Entomol. Soc. Am. 64:381-384.
- GIFFORD, F. A. 1960. Atmospheric dispersion, Nuclear Safety 1:56-69.

- HAMMACK, L., MA, M., and BURKHOLDER, W. E. 1976. Sex pheromone-releasing behavior in females of the dermestid beetle Trogoderma glabrum. J. Insect Physiol. 22:555-561.
- HARTSTACK, A. W., JR., WITZ, J. A., HOLLINGSWORTH, J. P., and BULL, D. L. 1976. SPERM - A sex pheromone emission and response model. Trans. ASAE 19: 1170-1174, 1180.
- HAWKINS, W. A. 1978. Effects of sex pheromone on locomotion in the male American cockroach, Periplaneta americana. J. Chem. Ecol. 4:149-160.
- HIENTON, T. E. 1974. Summary of investigations of electric insect traps. USDA Tech. Bull. No. 1498.
- HINZE, J. O. 1975. Turbulence. McGraw-Hill, New York.
- HIROOKA, Y., and SUWANAI, M. 1976. Role of insect sex pheromone in mating behavior. I. Theoretical consideration on release and diffusion of sex pheromone in the air. Appl. Entomol. Zool. 11:126-132.
- JUDEIKIS, H. S., and STEWART, T. B. 1976. Laboratory measurements of SO_2 deposition velocities on selected building materials and soils. Atmos. Environ. 10: 769-776.
- KAISLING, K. E. 1971. Insect olfaction. pp. 351-431, in L. M. Beidler (ed.). Handbook of Sensory Physiology IV. Springer-Verlag, Berlin, Heidelberg, New York.
- KAISLING, K. E., and PRIESNER, E. 1970. Die reichswelle des seidenspinners. Naturwiss. 57:23-28.
- KENNEDY, J. S. 1974. Pheromone-regulated anemotaxis in flying moths. Science 184:999-1001.
- KILLINGER, R. G., and OST, R. W. 1971. Pheromone-maze trap for cabbage looper moths. J. Econ. Entomol. 64:310-311.
- KNIPPLING, E. F., and MCGUIRE, J. U. 1966. Population models to test theoretical effects of sex attractants used for insect control. USDA Agric. Info. Bull. 308.
- LAMB, R. G., CHEN, W. H., and SEINFELD, J. H. 1975. Numerico-empirical analyses of atmospheric diffusion theories. J. Atmos. Sci. 32:1794-1807.

- LEWIS, T., and MACAULAY, E. D. M. 1976. Design and elevation of sex-attractant traps for pea moth, Cydia nigricana (Steph.), and the effect of plume shape on catches. Ecol. Entomol. 1:175-187.
- LUGG, G. A. 1968. Diffusion coefficients of some organic and other vapors in air. Anal. Chem. 40:1072-1077.
- LUNDBERG, W. O. 1961. Autoxidation and Antioxidants, I. Interscience, New York.
- MACAULAY, E. D. M., and LEWIS, T. 1977. Attractant traps for monitoring pea moth, Cydia nigricana (Fabr.). Ecol. Entomol. 2:279-284.
- MARKS, R. J. 1977. The influence of climatic factors on catches of the red bollworm Diaparopsis castanea Hampson (Lepidoptera:Noctuidae) in sex pheromone traps. Bull. Entomol. Res. 67:243-248.
- MARKS, R. J. 1978. The influence of pheromone trap design and placement on catch of the red bollworm of cotton Diaparopsis castanea Hampson (Lepidoptera:Noctuidae). Bull. Entomol. Res. 68:31-45.
- MAYER, M. S. 1973. Attraction studies of male Trichoplusia ni (Lepidoptera:Noctuidae) with new combination of olfactometer and pheromone dispenser. Ann. Entomol. Soc. Am. 66:1191-1196.
- MILLER, J. R., and ROELOFS, W. L. 1978. Sustained-flight tunnel for measuring insect responses to wind-borne sex pheromones. J. Chem. Ecol. 4:187-198.
- MONCHIECK, L., and MASON, E. A. 1961. Transport properties of polar gases. J. Chem. Phys. 35:1676-1697.
- MURLISS, J., and BETTANY, B. W. 1977. Night flight toward a sex pheromone source by male Spodoptera littoralis (Boisd.) (Lepidoptera, Noctuidae). Nature 268:433-435.
- NAKAMURA, K. 1976. The active space of the pheromone of Spodoptera litura and the attraction of adult males to the pheromone source. pp. 145-155, in T. Yushima (ed.). Insect Pheromones and Their Applications. National Inst. of Agri. Sci., Tokyo.
- NAKAMURA, K., and KAWASAKI, K. 1977. The active space of the Spodoptera litura (F.) sex pheromone and the pheromone component determining this space. App. Entomol. Zool. 12:162-177.

- NAKAMURA, K., and OYAMA, M. 1978. An equation for the competition between pheromone traps and adult females from adult males. Appl. Entomol. Zool. 13:176-184.
- PASQUILL, F. 1961. The estimation of the dispersion of windborne material. Meteorol. Mag. 90:33-53.
- PEREZ, R. P., and HENSLEY, S. D. 1973. Recapture of sugarcane borer (Diatraea saccharalis (F.)) males released at different distances from pheromone-baited traps. J. Agric. (Puerto Rico) 57:330-342.
- PROTTER, M. H., and MORREY, C. B., JR. 1966. Modern mathematical Analysis. Addison-Wesley, Reading, Mass.
- READ, I. S., and HAINES, C. P. 1976. The functions of the female sex pheromones of Ephestia cautella (Walker) (Lepidoptera, Phycitidae). J. Stored Prod. Res. 12:49-53.
- ROELOFS, W. L. 1975. Manipulating sex pheromones for insect suppression, pp. 41-59, M. Jacobson (ed.). in Insecticides of the Future. Marcel Dekker, Inc., New York.
- ROELOFS, W. L. 1978. Threshold hypothesis for pheromone perception. J. Chem. Ecol. 4:685-699.
- SANDERS, C. J., WALLACE, D. R., and LUCUIK, G. S. 1978. Flight activity of female eastern spruce budworm (Lepidoptera: Tortricidae) at constant temperatures in the laboratory. Can. Entomol. 110:627-632.
- SCHNEIDER, D., BLOCK, B. C., BOECKH, J., and PRIESNER, E. 1967. Die reaktion des männlichen seidenspinner auf bombykol und seine isomerer: elektroantennogram und verhalten. Z. Vergl. Physiol. 54:192-209.
- SEARS, F. W. 1958. Mechanics, Wave Motion, and Heat. Addison-Wesley, Reading, Mass.
- SHAPAS, T. J. 1977. Trogoderma sex pheromone, 14 methyl-8-hexadecenal. Theoretical communication distances, roles with behavioral mechanisms in reproductive isolation, and use in pathogen dissemination for population suppression. PhD. Dissertation, Univ. of Wisc.
- SHOREY, H. H. 1966. The biology of Trichoplusia ni (Lepidoptera: Noctuidae). IV. Environmental control of mating. Ann. Entomol. Soc. Am. 59:502-506.

- SHOREY, H. H., and GASTON, L. K. 1965. Sex pheromones of noctuid moths. VIII. Orientation to light by pheromone-stimulated males of Trichoplusia ni (Lepidoptera: Noctuidae). Ann. Entomol. Soc. Am. 58:833-836.
- SHOREY, H. H., GASTON, L. K., and SARRIO, C. A. 1967. Sex pheromone of noctuid moths. XIV. Feasibility of behavioral control by disrupting pheromone communication in cabbage loopers. J. Econ. Entomol. 60:1541-1545.
- SHOREY, H. H., and MCKELVEY, J. J., JR. 1977. Chemical Control of Insect Behavior: Theory and Application. Wiley-Interscience, New York.
- SHOWERS, W. B., REED, G. L., and OLOUMI-SADEGHI, H. 1974. European corn borer: Attraction of males to synthetic lure and to females of different strains. Environ. Entomol. 3:51-58.
- SILHACEK, D. L., and MILLER, G. L. 1972. Growth and development of the Indian meal moth Plodia interpunctella (Lepidoptera: Phycitidae). Ann. Entomol. Soc. Am. 65:466-468.
- SKELLAND, A. H. P. 1974. Diffusional Mass Transfer. John Wiley & Sons, New York.
- SOWER, L. L., GASTON, L. K., and SHOREY, H. H. 1971. Sex pheromones of noctuid moths. 26. Female release rate, male response threshold, and communication distance of T. ni. Ann. Entomol. Soc. Am. 64:1148-1156.
- SOWER, L. L., LONG, J. S., VICK, K. W., and COFFELT, J. A. 1973. Sex pheromone of the Angoumois grain moth: Effects of habituation on the response of the male. Ann. Entomol. Soc. Am. 66:991-995.
- SOWER, L. L., and FISH, J. C. 1975. Rate of release of the sex pheromone of the female Indian meal moth. Environ. Entomol. 4:168-169.
- SOWER, L. L., TURNER, W. K., and FISH, J. C. 1975. Population-density-dependent mating frequency among Plodia interpunctella (Lepidoptera: Phycitidae) in the presence of synthetic sex pheromone with behavioral observations. J. Chem. Ecol. 1:335-342.
- SUTTON, O. G. 1953. Micrometeorology. McGraw-Hill, New York.
- TAYLOR, L. R. 1963. Analysis of the effects of temperature on insects in flight. J. Anim. Ecol. 32:99-117.

- THOMPSON, R. F., and SPONCER, W. A. 1966. Habituation: A model phenomenon for the study of neuronal substrates of behavior. Psychol. Rev. 73:16-43.
- TRAYNIER, R. M. M. 1968. Sex attraction in the Mediterranean flour moth, Anagasta kühniella: Location of the female by the male. Can. Entomol. 100:5-10.
- VEIGELE, W. J., and HEAD, J. H. 1978. Derivation of the Gaussian plume model. J. Air Poll. Control Assoc. 28:1139-1141.
- VICK, K. W., and SOWER, L. L. 1973. (Z)-9,12-Tetradecadien-1-ol acetate: An inhibition of the response to the sex pheromone of Plodia interpunctella. J. Econ Entomol. 66:1258-1260.
- VICK, K. W., COFFELT, J. A., and SULLIVAN, M. A. 1978. Disruption of pheromone communication in the Angoumois grain moth with synthetic pheromone. Environ. Entomol. 7:528-531.
- VICK, K. W., KVENBERG, J., COFFELT, J. A., and STEWARD, C. 1979. Investigation of sex pheromone traps for simultaneous detection of Indian meal moths and Angoumois grain moths. J. Econ. Entomol. 72:245-249.
- VISSEER, J. H. 1976. The design of a low-speed wind tunnel as an instrument for the study of olfactory orientation in the Colorado beetle (Leptinotarsa decemlineata). Entomol. Exp. & Appl. 20:275-288.
- VON REICHMUTH, C., WOHLGEMUTH, R., LEVINSON, A. R., and LEVINSON, H. Z. 1976. Untersuchungen über den Einsatz von pheromonbeköderten klebefallen zur Bekämpfung von motten im Vorratsschutz. Z. Angew. Entomol. 82:95-102.
- VON REICHMUTH, C., SCHMIDT, H. U., LEVINSON, A. R., and LEVINSON, H. Z. 1978. Die fängigkeit pheromonbeköderte Klebefallen für Speichermaßen (Ephestia elutella Hubn.) in unterschiedlich dicht defallenen Gertreidelägern. Z. Angew. Entomol. 86:205-212.
- WALL, C., and PERRY, J. N. 1978. Interactions between pheromone traps for the pea moth, Cydia nigicana (F.). Entomol. Exp. & Appl. 24:155-162.
- WILSON, E. O., BOSSERT, W. H., and REGNIER, F. E. 1969. A general method for estimating threshold concentrations of odorant molecules. J. Insect Physiol. 15:597-610.

WOLF, W. W., KISHABA, A. N., HOWLAND, A. F., and HENNEBERRY, T. J. 1967. Sand as a carrier for synthetic sex pheromone of cabbage looper used to bait black light and carton traps. J. Econ. Entomol. 60:1182-1184.

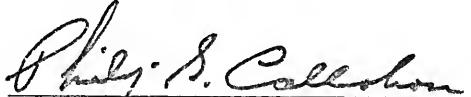
WRIGHT, R. H. 1958. The olfactory guidance of flying insects. Can. Entomol. 90:81-89.

BIOGRAPHICAL SKETCH

The author was born on Valentine's day 1948. From 1966 to 1970 he attended New Mexico State University on a National Merit Scholarship, obtaining a B.S. in physics and a B.S. in mathematics. Concurrently, he worked part time at the Physical Science Laboratory in Las Cruces, New Mexico, testing quality control in telemetry antennas for rockets. From 1970 to 1973 he participated in the graduate physics program at the University of Florida, majoring in biophysics. Then he became a laboratory technician at the U. S. Department of Agriculture, Insect Attractants, Behavior, and Basic Biology Research Laboratory in Gainesville, Florida.

A master's thesis in 1976 and this dissertation both stem from work performed under this tenure.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



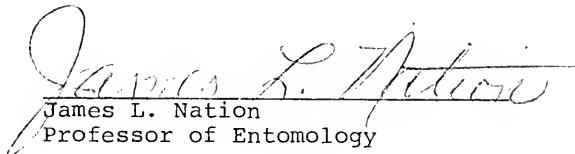
Philip S. Callahan, Chairman
Professor of Entomology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Marion S. Mayer
Associate Professor of Entomology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



James L. Nation
Professor of Entomology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Robert J. Cohen
Robert J. Cohen
Associate Professor of
Biochemistry

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John F. Anderson
John F. Anderson
Associate Professor of Zoology

This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August 1979

Jack L. Fry
Dean College of Agriculture

Dean, Graduate School

UNIVERSITY OF FLORIDA



3 1262 08553 1555